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A new genus for an aquatic ranid (Amphibia, Anura) from Sri Lanka

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A new monotypic genus is erected for the species *Rana corrugata* Peters, 1863, a ranid endemic of the island of Sri Lanka. This species shares the paedomorphic condition of the retention of a lateral-line system in adults with two other genera of Ranidae, *Euphlyctis* and *Occidozyga*. It shares with many species of the genus *Limnonectes* the presence of odontoid "fangs" on the anterior lower jaw of males. Despite these similarities, the new genus is not closely related to the three genera above, and appears to represent a new, independent lineage within the South Indian ranids. It is here provisionally referred to a new subfamily of the family Ranidae. This study provides an opportunity for a brief review of the distribution of several interesting characters among several genera of Ranidae, including characters related with an aquatic mode of life (general morphology, lateral-line system, coloration of the back of thighs), male secondary characters (fangs, large head, dorsal cephalic knob, size dimorphism, nuptial pads, vocal sacs, advertisement and territorial calls), amplectic position, parental care and egg coloration.

ABBREVIATIONS

Measurements EL, eye length, EN, distance from front of eye to nostril, FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe; FL, femur length (from vent to knee), FLL, forelimb length (from elbow to base of outer palmar tubercle), FOL, foot length (from base of inner metatarsal tubercle to tip of fourth toe), HAL, hand length (from base of outer palmar tubercle to tip of third finger), HL, head length (from back of mandible to tip of snout), HW, head width, IBE, distance between back of eyes, IFE, distance between front of eyes, IMT, length of inner metatarsal tubercle, IN, internarial space, ITL, inner toe length, IUE, minimum distance between upper eyelids, MBE, distance from back of mandible to back of eye, MFE, distance from back of mandible to front of eye, MN, distance from back of mandible to nostril, MTFF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe, MTTF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe, *nm*, no measurement taken, NS, distance from nostril to tip of snout, SL, distance from front of eye to tip of snout, SVL snout-vent length TFOL, length of tarsus and foot (from base of tarsus to tip of fourth toe), TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe, TL, tibia length, TW, maximum tibia width, UEW, maximum width of upper eyelid

Museums, collections and persons. – AD, Alain Dubois, AMO, Annemarie Ohler; BMNH, Natural History Museum, London, United Kingdom, MNHN, Muséum National d'Histoire Naturelle, Paris, France, MV, Michael Veith collection, Mainz, Germany, NHMB, Naturhistorisches Museum Basel, Basel, Switzerland, NMW, Naturhistorisches Museum, Wien, Austria; NRM, Swedish Museum of Natural History, Stockholm, Sweden, ZMB, Zoologisches Museum, Berlin, Germany

Introduction

Taxonomy of the family Ranidae Rafinesque-Schmaltz, 1814 is among the most challenging in anuran amphibians. This is due in part to the existence of groups including many sibling species (see e.g.: Dubois, 1977, Matsui et al., 1993, Emerson & Ward, 1998), and of numerous cases of convergence between species belonging to distinct lineages (see e.g.: Ohler & Dubois, 1989; Bossuyt & Milinkovitch, 2000, Marmayou et al., 2000).

Particularly confused and controversial is the taxonomy of the so-called genus *Rana* Linnaeus, 1758 (sensu Boulenger, 1920), that has until now been used to group frogs belonging to various lineages but showing "generalized" morphologies and unspecialized plesiomorphic characters. As far back as in 1915, however, Bolkay had proposed to remove from this genus several species with a forked omosternum and other unusual characters for the genus *Rana*, and to place them in the new genus *Fejervarya*. A similar proposal was made by Deckert (1938), followed by Laurent (1950) and others, who used the generic nomen *Dicroglossus* Günther, 1860 for these frogs; in particular, for several decades, the common African frog now known as *Hoplobatrachus occipitalis* (see e.g. Kosuch et al., 2001) was referred to under the nomen *Dicroglossus occipitalis*. However, this was ignored by many other authors, especially those working on the Asian fauna (see e.g.: Bourret, 1942, Liu, 1950, Inger, 1954, 1966, 1985; Liu & Hu, 1961; Taylor, 1962; etc.). Dubois (1974) was the first author to use the nomen *Dicroglossus* for Asian frogs, before showing (Dubois, 1975) that this nomen was a strict junior synonym of *Euphlyctis* Fitzinger, 1843. The same author subsequently distributed the ranid species with forked omosternum in several subgenera of *Rana* (Dubois, 1981), and later in several distinct genera (Dubois, 1987*b*, 1992). Among the five subgenera he recognized in *Limnonectes* Fitzinger, 1843 in 1987, Dubois (1992) raised *Hoplobatrachus* Peters, 1863 and *Taylorana* Dubois, 1987 to the rank of distinct genera, and Dubois & Ohler (2000) did the same for *Fejervarya*. Ohler & Dubois (1999) showed that *Bourretia* Dubois, 1987 was a junior synonym of *Elachyglossa* Andersson, 1916. Therefore, according to these latter authors, the genus *Limnonectes* is now understood as including two subgenera, *Elachyglossa* and *Limnonectes*, the latter with three species-groups (Dubois, 1987*b*: 63).

In the genus *Limnonectes*, the *Limnonectes kuhlii* group corresponds to the *Ranae kuhlianae* of Boulenger (1920). Adult males of these frogs are devoid of vocal sacs and nuptial pads, but have very enlarged heads and strong tooth-like prominences ("fangs") on the anterior lower jaw. All species of this group occur in South-East Asia (Indonesia, Malaysia, Indochina and southern China), except for one, originally described by Peters (1863) as *Rana corrugata*, which lives only in Sri Lanka. When he first erected the *L. kuhlii* group, Dubois (1987*b*) followed Boulenger (1920) in including this Sri Lankan species in this group, although he had never had an opportunity to examine a specimen of this species.

However, as soon as he first saw this species alive in the field, on 30 June 1999 in Morningside in Sri Lanka, he realized that all published descriptions of this species (PETERS, 1863, GÜNTHER, 1864; BOULENGER, 1882, 1890, 1920; KIRTISINGHE, 1957, DUTTA & MANAMENDRA-ARACHCHI, 1996) were incomplete or even partly inaccurate, and that the external characters of this species (see below) were in several respects quite different from those of the *L. kuhlii* group and justified the exclusion of this species not only from this group but also from the genus *Limnonectes*.

Recently, some molecular cladistic data were published concerning these frogs. After an analysis of parts of the mitochondrial ribosomal 12S and 16S genes of several species, EMERSON et al. (2000: 136) wrote that "the fanged frogs constitute a monophyletic group" and that "it seems appropriate, in the future, to refer to these frogs as members of the genus *Limnonectes*". While doing so, however, they did not provide a list of taxa that they referred to this genus, so that one can infer that they probably adopted DUBOIS's (1992) concept of the latter. However, they provided (EMERSON et al., 2000: 131) a "definition" of "fanged frogs" that does not apply to all species or species-groups of this genus. All characters listed in this "definition" either apply to some of these taxa only (see e.g. BOULENGER, 1920, DUBOIS, 1987*b*, 1992), such as fangs and "voicelessness" (see below) in adult males, sexual size dimorphism or parental care. However, using this "definition", it is quite clear that *Rana corrugata* should be included in the genus *Limnonectes*. These authors did not, however, consider this species in their study.

Other recent studies provided additional data in this respect. Using mitochondrial 12S and 16S rRNA gene sequences, VENCES et al. (2000) and DELORME et al. (submitted) found that *Rana corrugata* is not cladistically a member of the group including *L. kuhlii*, the type-species of *Limnonectes*. BOSSUYT & MILINKOVITCH (2000) found a similar result using the same genes but also two nuclear DNA gene sequences. These data confirm the morphological interpretation of *R. corrugata* as not belonging in the genus *Limnonectes*.

On the basis of the molecular phylogenetic data mentioned above, DELORME et al. (submitted) followed DUBOIS (1992) in recognizing in the Ranidae a subfamily Dicroglossinae Anderson, 1871, and, within the latter, a tribe Limnonectini Dubois, 1992 for the genera *Limnonectes* and *Taylorana*. They excluded *Rana corrugata* from this tribe, suggesting that the latter deserves erection of a new genus, that represents an hitherto unsuspected new clade within the Ranidae. In the frame of the current "working taxonomy" of the latter family (DUBOIS, 1999), we suggest that this clade be recognized provisionally as a new subfamily, and we hereby propose a diagnosis and a nomen both for this subfamily and for its unique genus. In order to facilitate the discussion below, we introduce the new nomina first, so that we can use them in the rest of the paper. According to Kelum Manamendra-Arachchi (personal communication), some differences exist between low and high altitude populations currently referred to this species, so that later two distinct taxa (species or subspecies) might have to be distinguished. In order to clarify the nomenclatural decisions that might have to be taken in this respect, we provide a detailed redescription of one of the three original syntypes of this nominal species, that we hereby designate as lectotype. In the final part of the paper, we discuss the distribution of some morphological characters among several genera of Ranidae, that give support to our taxonomic decisions.

Material and methods

The list of specimens examined and measured is given below in tab. 4 and in app. 1.

Twenty-two measurements of adult and young specimens were taken by AMO with a slide calliper to the nearest 0.1 mm, or, for values below 5 mm, with an ocular micrometer to the nearest 0.01 mm. The list of measurements is given above under *Abbreviations*

In order to facilitate comparisons, the description's methodology and plan used in the lectotype description below were the same as those used in previous works on Asian anurans (Dubois & Ohler, 1998, 1999, 2000; Ohler & Dubois, 1999, Bossuyt & Dubois, 2001; Veith et al., 2001; Dubois et al., 2001). The webbing formula is given according to Myers & Duellman (1982) and the tadpole keratodont formula according to Dubois (1995).

Morphometric analyses and graphs were made using the SPSS statistical programs for personal computers (Norusis, 1992, Anonymous, 1999). We used principal component analysis using varimax rotation (Anonymous, 1999: 426) to show morphological distinctiveness of the new genus and canonical discriminant analysis to indicate morphological discrimination from the subgenera and species-groups of *Limnonectes*. Oneway analysis using Scheffe tests were performed on ranked ratios of all measurements between the seven genera of Ranidae compared in tab. 1. Detailed results of this analysis can be communicated upon request by the authors; they are not provided here because of space limitations.

Taxonomic novelties

Subfamily **Lankanectinae** nov

Type-genus, by present designation. – *Lankanectes* gen. nov.

Diagnosis. This subfamily is distinguished from all other subfamilies of Ranidae by the following combination of characters: (1) omosternum forked at base, (2) vomerine teeth present, (3) median lingual process absent, (4) femoral gland absent, (5) extremities of digits pointed or slightly rounded, not enlarged; (6) tarsal fold present; (7) lateral-line system present in adult, (8) head and back covered by a network of ridges, (9) adult male without nuptial pads, but with fangs and internal vocal sacs, (10) eggs pigmented, (11) tadpole with ventral mouthparts, keratodont formula 2/3.

Distribution. So far, this subfamily is known only from the island of Sri Lanka

Genus **Lankanectes** nov.

Type-species, by present designation – *Rana corrugata* Peters, 1863.

Diagnosis. – This genus is distinguished from all other genera of Ranidae by the following combination of characters: (1) omosternum forked at base; (2) size medium (adult SVL 33-65 mm); (3) internarial distance shorter than distance between upper eyelids; (4) upper eyelids covered with numerous round warts; (5) canthus rostralis indistinct, loreal region slightly convex; (6) edge of lower jaw without transverse bands; (7) tympanum indistinct; (8) vomerine teeth present, (9) median lingual process (see GRANT et al., 1997) absent, (10) extremities of fingers pointed, of toes slightly rounded; (11) finger II longer than finger I; (12) no distal subarticular tubercles on fingers III and IV; (13) inner palmar tubercle very small, rounded, on base of metacarpus, (14) outer palmar tubercle very small, rounded, similar and of same size as inner; (15) legs strong, heels far apart when hind legs are placed at right angle with body, (16) tarsal fold present, well developed, (17) inner metatarsal tubercle flat, elongate, (18) outer metatarsal tubercle absent; (19) tarsal tubercle absent; (20) femoral glands absent; (21) lateral-line system present in adult, (22) dorsal parts covered with a network of ridges, (23) fejervaryan line (see DUBOIS & OHLER, 2000, and DUBOIS et al., 2001) absent; (24) rear part of thighs marbled, without longitudinal white and dark lines; (25) adult male with fangs and internal vocal sacs, without nuptial pads, (26) eggs pigmented, (27) tadpole with ventral mouthparts, keratodont formula 2/3

Comparisons. – Detailed comparisons of this genus with six other genera of Asian Ranidae with forked omosternum are provided in tab. 1. Of particular relevance are the comparisons with three of them, which in several characters rather closely resemble the new genus. *Lankanectes* shares several characters with the Asian ranid genera *Euphlyctis* and *Occidozyga* Kuhl & Van Hasselt, 1822; in particular, in these three genera a lateral line system is present on the body of adults, a rare character in the Ranidae (see below). It is distinguished from these two genera by a combination of characters (see tab. 1), among which the following ones in particular may be highlighted: (1) internarial distance shorter than distance between upper eyelids (instead of subequal or longer); (2) loreal region slightly convex (instead of slightly concave); (3) network of numerous transverse folds on the whole of back and head (absent in the other two genera); (4) inner metatarsal tubercle flat (instead of digit-like), (5) rear part of thighs marbled (instead of showing a longitudinal white line underlined by a dark line), (6) adult male with fangs on the anterior lower jaw. This last character is shared by the new genus and some species of the genus *Limnonectes*, but *Lankanectes* differs from the latter in several other characters (see tab. 1), including (1) internarial distance shorter than distance between upper eyelids (instead of subequal or longer), (2) loreal region slightly convex (instead of concave); (3) network of numerous transverse folds on the whole of back and head (absent in *Limnonectes*), (4) upper eyelids covered with numerous round warts (instead of bearing only a few round warts in their rear part), (5) finger II longer than finger I (instead of shorter or subequal), (6) lateral line system present in adult (instead of absent)

Generic content and distribution. – For the time being, a single species, *Lankanectes corrugatus* (Peters, 1863), an endemic of the island of Sri Lankan, is known in this genus. However, as mentioned above, this species might prove later to be heterogeneous and to consist in fact of

Table 1 Some diagnostic morphological characters of seven Asian genera of the family Ranidae with omosternum forked at base. See DUBOIS (1995) for the definition of the tadpole's condensed collective keratodont formula (CCKF), i.e. minimum-maximum numbers of keratodont rows on upper/lower lips of tadpoles observed in the taxon. See OHLER & DUBOIS (1999) for the definition of categories of digital disks in the Ranidae.

Subfamily	Dicroglossinae Anderson, 1871	Dicroglossinae Anderson, 1871	Dicroglossinae Anderson, 1871	Occidozyginae Fei, Ye & Huang, 1991	Occidozyginae Fei, Ye & Huang, 1991	Nyctibatrachinae Blommers-Schlösser, 1993	Lankanectinae subfam. nov.
Tribe	Dicroglossini Anderson, 1871	Limnonectini Dubois, 1992	Limnonectini Dubois, 1992		-		
Genus	*Euphlyctis* Fitzinger, 1843	*Limnonectes* Fitzinger, 1843	*Taylorana* Dubois, 1987	*Occidozyga* Kuhl & Van Hasselt, 1822	*Phrynoglossus* Peters, 1867	*Nyctibatrachus* Boulenger, 1882	*Lankanectes* gen. nov.
Type-species	*Rana leschenaultii* Duméril & Bibron, 1841 by original designation (FITZINGER, 1843: 31)	*Rana kuhlii* Tschudi, 1838, by original designation (FITZINGER, 1843: 31)	*Polypedates hascheanus* Stoliczka, 1870, by original designation (DUBOIS, 1987b: 63)	*Rana lima* Gravenhorst, 1829, by subsequent designation of STEJNEGER (1925: 33)	*Phrynoglossus martensii* Peters, 1867 by original monotypy (PETERS, 1867: 29)	*Nyctibatrachus major* Boulenger, 1882, by subsequent designation of MYERS (1942: 54)	*Rana corrugata* Peters, 1863, by original designation (hoc loco)
Adult male SVL (mm)	40-95	35-150	25-39	19-26	18-30	3-46	33-65
Adult female SVL (mm)	45-130	35-135	24-37	26-35	22-45	14-47	44-59
Internarinal distance	Longer than distance between upper eyelids	Longer than or equal to distance between upper eyelids	Longer than distance between upper eyelids	Subequal to distance between upper eyelids	Longer than distance between upper eyelids	Shorter than distance between upper eyelids	Shorter than distance between upper eyelids
Upper eyelids	Covered with numerous round warts	Bearing a few round warts in their rear part	Bearing a few round warts in their rear part	Covered with numerous round warts	Covered with a few indistinct round warts	Without warts or covered with numerous round warts	Covered with numerous round warts
Canthus rostralis	Indistinct	Distinct or little distinct	Little distinct	Indistinct	Indistinct	Indistinct or little distinct	Indistinct
Loreal region	Slightly concave	Concave	Flat	Slightly concave	Slightly convex	Slightly convex	Slightly convex
Coloration of edge of lower jaw	Without transverse bands	With transverse bands	With transverse bands	Without transverse bands	Without transverse bands	Without transverse bands	Without transverse bands
Tympanum	Distinct	Distinct or indistinct	Distinct	Indistinct	Indistinct	Indistinct or little distinct	Indistinct
Extremities of digits	Pointed, not enlarged	Rounded, those of toes sometimes dilated as small disks bearing a dorso-terminal fold	Slightly enlarged with a rudimentary dorso-terminal fold	Pointed, not enlarged	Rounded, sometimes slightly enlarged	Disks bearing dorso terminal folds	Extremities of fingers pointed, or toes slightly rounded
Relative length of fingers I and II	Finger II longer than finger I	Finger II shorter than or as long as finger I	Finger II shorter than finger I	Fingers I and II subequal	Finger II shorter than finger I	Finger II longer than finger I	Finger II longer than finger I
Distal subarticular tubercles on fingers III and IV	Small	Indistinct	Small	Absent	Absent	Indistinct	Absent
Inner palmar tubercle	Medium, oval, on the base of metacarpus	Medium or large, on base of metacarpus or on the whole of it	Medium, oval, on half of metacarpus	Small, rounded, prominent, on base of metacarpus	Small, oval, on base of metacarpus	Small, oval, rather prominent, on base of metacarpus	Very small, rounded, on base of metacarpus
Outer palmar tubercle	Indistinct	Elongate, half smaller than inner palmar tubercle or of same size	Oval, a little smaller than inner	Small, rounded prominent, of same size as inner palmar tubercle	Small, oval, of same size as inner palmar tubercle	Oval, about half-size of inner palmar tubercle	Very small, rounded, of same size as inner palmar tubercle

Table 1 (continued)

Genus	*Euphlyctis* Fitzinger, 1843	*Limnonectes* Fitzinger, 1843	*Taylorana* Dubois, 1987	*Occidozyga* Kuhl & Van Hasselt, 1822	*Phrynoglossus* Peters, 1867	*Nyctibatrachus* Boulenger, 1882	*Lankanectes* gen. nov.
Hind legs	Rather strong and short	Strong or narrow, short or long	Moderately strong, rather short	Rather strong, short	Rather strong, short	Strong, short	Very strong, short
Distance between heels when hind legs are placed at right angle with body	Heels far apart	Heels in contact or overlapping	Heels in contact	Heels far apart	Heels far apart	Heels far apart	Heels far apart
Tarsal fold or ridge	Present, moderate	Present, well developed	Indistinct	Present, moderate	Present, well developed	Present, well developed	Present, well developed
Inner metatarsal tubercle	Finger-like, elongate	Flat, elongate	Very prominent, elongate	Finger-like, very prominent	Oval, very prominent	Long, oval, prominent	Flat, elongate
Outer metatarsal tubercle	Absent	Absent	Absent	Present	Absent	Absent	Absent
Tarsal tubercle	Absent	Absent	Absent	Present	Absent	Absent	Absent
Femoral glands	Absent	Absent	Absent	Absent	Absent	Present	Absent
Lateral line system in adult	Present	Absent	Absent	Present	Absent	Absent	Present
Longitudinal dorsal glandular folds	Absent	Present or absent	Present	Absent	Absent	Absent	Absent
Network of ridges on back and head	Absent	Absent	Absent	Absent	Absent	Absent	Present
Coloration of rear part of thighs	Longitudinal white line underlined by dark line	Marbled	Marbled	Longitudinal white line underlined by black line	Marbled or spotted	Marbled	Marbled
Sexual size dimorphism	Males smaller than females	Absent or males larger than females	Absent	Males smaller than females	Males smaller than females	Absent	Absent
Enlargement of head in adult male	Absent	Present or absent	Present	Absent	Absent	Absent	Absent
Fangs in adult male	Absent	Present or absent	Present, small	Absent	Absent	Absent	Present
Vocal sacs in adult male	Present, black, protruding through slits on ventral sides on throat	Absent or present, internal, with folds on throat	Absent	Present, internal, with folds on throat	Present, internal with folds on throat	Present, internal, with folds on throat	Present, internal, without folds on throat
Male advertisement call	Present	Absent or present	Present	Present	Present	Present	Present
Nuptial pads in adult male	Absent	Absent	Absent	Present	Present	Present	Absent
Amplectic position	Axillary	?	?	Axillary	Lumbar	?	?
Egg coloration	Pigmented	Pigmented	Unpigmented	Pigmented	Unpigmented	Pigmented or not	Pigmented
Mode of development	Tadpole	Tadpole or endotroph	Endotroph	Tadpole	Tadpole	Tadpole	Tadpole
Parental care	Absent	Absent or present	Present	Absent	Absent	Absent	Absent
Tadpoles O/KF	2	?3 ?3	-	0/0	0/0	0/0	2/3
References for characters	BOULENGER, 1920; DECKERT, 1938, DUBOIS, 1986	BOULENGER, 1920, DECKERT, 1938	BOULENGER, 1920; TAYLOR, 1962, YANG, 1991, OHLER et al., 1999	BOULENGER, 1890 DECKERT, 1938, YANG, 1991	DECKERT, 1938 INGER, 1966; YANG, 1991	CLARKE, 1983, INGER et al., 1984	BOULENGER, 1920; DECKERT, 1938, KIRTISINGHE, 1957 DUTTA & MANAMENDRA-ARACHCHI, 1996

two species or subspecies. In order to facilitate further works in this respect, we provide below a detailed redescription of the lectotype, designated herein, of *Rana corrugata* Peters, 1863.

Vernacular name – We propose to use the name "lankanects" as vernacular name for these frogs, and "limnonects" for frogs of the genus *Limnonectes*.

Etymology of the generic nomen – The new generic nomen, of masculine grammatical gender, is derived from the frog generic nomen *Limnonectes* Fitzinger, 1843, and from the name of the island of Sri Lanka. It suggests that these frogs are limnonect-like frogs endemic of this island.

Lectotype description

Lectotype, by present designation, of *Rana corrugata* Peters, 1863: ZMB 4897, adult male (fig. 1), collected by J. Nietner in "Rambodde" (Ramboda; 07°03'N, 80°14'E; 1310 m) (Dutta & Manamendra-Arachchi, 1996: 12), Sri Lanka.

(A) Size and general aspect. (1) Specimen of moderate size (SVL 44.0 mm), body stout.

(B) Head. (2) Head rather large, wider (HW 17.2 mm) than long (HL 16.8 mm, MN 15.3 mm; MFE 12.8 mm; MBE 8.3 mm), convex. (3) Snout rounded, slightly protruding; its length (SL 6.03 mm) longer than horizontal diameter of eye (EL 5.25 mm). (4) Canthus rostralis indistinct, loreal region convex; angle of loreal region with upper face of head flared. (5) Interorbital space flat, broader (IUE 4.02 mm) than upper eyelid (UEW 2.01 mm) and than internarial distance (IN 2.46 mm); distance between front of eyes (IFE 6.68 mm) about half of distance between back of eyes (IBE 12.76 mm). (6) Nostrils oval, with small flap of skin laterally; closer to eye (EN 2.66 mm) than to tip of snout (NS 3.37 mm). (7) Pupil not observable. (8) Tympanum indistinct (TYD *nn*, TYE *nn*). (9) Pineal ocellus absent. (10) Maxillary teeth present; vomerine ridge present, bearing 2 small teeth, posterior to choanae, with an angle of 40° relative to body axis, closer to each other than to choanae, longer than distance between them. (11) Tongue chordate, deeply emarginate, without lingual process, covered by numerous small papillae. (12) A dermal, non glandular supratympanic fold, distinct, from eye to shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

(C) Forelimbs. (16) Arm short, fore-arm (FLL 8.6 mm) shorter than hand (HAL 8.8 mm), not enlarged. (17) Fingers short and rather strong (TFL 4.21 mm). (18) Relative length of fingers, shortest to longest: I < IV < II < III. (19) Tips of fingers pointed, bearing small, rounded terminal notch, not enlarged. (20) Fingers without dermal fringe and webbing. (21) Subarticular tubercles prominent, conical, single; distal tubercle of finger III and IV absent. (22) Prepollex small (size of subarticular tubercles), rounded, distinct; a single, small, round inner palmar tubercle on the base of metacarpus, outer palmar tubercle similar and of same size as inner; supernumerary tubercles absent.

(D) Hindlimbs. (23) Shank two times longer (TL 18.7 mm) than wide (TW 10.1 mm), shorter than thigh (FL 19.7 mm) and than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 19.8 mm). (24) Toes short, rather thin, toe IV (FTL 10.8) longer than third of distance from base of tarsus to tip of toe IV (TFOL 28.5 mm). (25) Relative length of

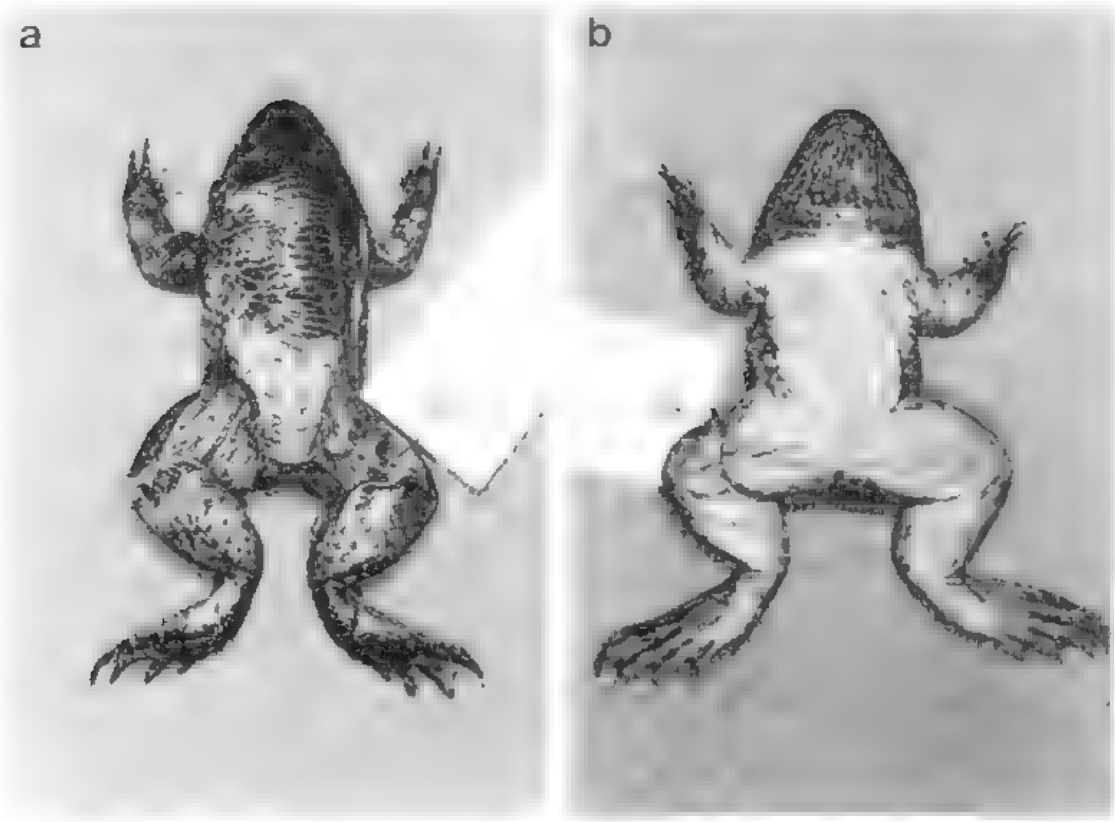

Fig. 1 Lectotype of *Rana corrugata* Peters, 1863, ZMB 4897, adult male (SVL 44 0 mm). (a) Dorsal view. (b) Ventral view

toes, shortest to longest I < II < V < III < IV (26) Tips of toes pointed, bearing enlarged knob terminally (27) Webbing complete I 0 - 0 II 0 - 0 III 0 0 IV 0 0 V (WTF 7 24 mm; WFF 6.32 mm; WI 6 58 mm; WII 5 00 mm, MTTF 13 68 mm; MTFF 14.47 mm; TFTF 5.66 mm, FFTF 8.42 mm). (28) Dermal fringe along toe V absent. (29) Subarticular tubercles conical, all present. (30) Inner metatarsal tubercle elongate, very prominent, shovel-shaped, its length (IMT 3 18 mm) 2 times in length of toe I (ITL 6 35 mm). (31) Tarsal fold present, from inner metatarsal tubercle to before tibio-tarsal articulation. (32) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin (33) Dorsal and lateral parts of head and body: smooth skin forming numerous regularly arranged folds, transversally arranged on back, longitudinally arranged between eyes; between these folds presence of round indistinct warts; laterally on posterior part of back, 4-5 symmetrically arranged pairs of prominent, medium sized warts, flanks smooth (34) Latero-dorsal folds absent (35) Dorsal parts of limbs forelimb with transversal foldings; thigh with flat warts, leg and tarsus with glandular warts bearing horny spinules. (36) Ventral parts of head, body and limbs throat with longitudinal foldings, chest, belly and thigh smooth, fejervaryan line absent, lateral-line system indistinct (37) Macroglands absent

(F) Coloration in alcool. (38) Dorsal and lateral parts of head and body, dorsal parts of head and dorsum and upper part of flank dark brown with top of folds whitish (discoloration), a blackish brown band between eyes. (39) Dorsal parts of limbs, dorsal part of forelimb, of thigh, of shank and of foot dark brown with indistinct darker brown bands, posterior part of thigh brown with blackish triangle around vent. (40) Ventral parts of head, body and limbs, throat and margin of throat dark brown; chest and belly whitish with some dark brown spots; thigh whitish; webbing whitish with dark brown marblings.

(G) Male secondary sexual characters. (41) Nuptial spines absent. (42) Vocal sacs present, indistinct on throat; distinct, rounded, paired openings, posteriorly on mouth floor. (43) Other male secondary sexual characters: toothlike projections (fangs) at the front of lower jaw.

Discussion

Morphological and morphometric analyses

Morphological comparison between the genus *Lankanectes* and 6 other genera of Asian Ranidae with omosternum forked at base is given in tab. 1. Some of the major differences between the new genus and these genera were already mentioned in the diagnoses of the new taxa given above, and are not repeated here.

Morphometric comparisons also support the distinctiveness of the new taxon. As we have already stressed elsewhere (e.g., Dubois et al., 2001), in many anuran groups the general "body shape" gives good clues regarding generic classification and allocation of species to genera. Once again we confirm this statement in the present study. On the basis of 22 measurements (see *Material and methods* above), we compared *Lankanectes corrugatus* with several species belonging to the four subgenera and species-groups currently recognized in the genus *Limnonectes*. Besides, we also thought useful to compare this species with members of several other genera discussed above (*Euphlyctis*, *Occidozyga* and *Phrynoglossus*) and also with the genus *Nyctibatrachus*, an endemic of southern India. The results are shown in tab. 2 and fig. 2. *Lankanectes corrugatus* appears as a well-distinguished group, as much as the other genera considered here. This result is confirmed by the canonical discriminant analysis based on 19 measurements and involving *Lankanectes* and the four subgroups (subgenera or species-groups) currently recognized in the genus *Limnonectes* (tab. 3, fig. 3).

Oneway analysis using the Scheffe test shows significant differences in various characters between *Lankanectes* specimens and specimens of the 8 other taxa studied. The new genus can be distinguished from all 4 subgroups of *Limnonectes* studied by a shorter head (HL), shorter eye-nostril distance (EN) and shorter shank (TL). Members of the subgenus *Elachyglossa* also have larger head (HW), greater internarial distance (IN) and more developed webbing (IFTF). The frogs of the *grunniens* species-group are significantly larger (SVL) than *Lankanectes* specimens and show differences in eye position (MFE, IBE). As compared to the *kuhlii* species-group, the new genus has significantly smaller (HW) and shorter head (beside HL, MN is significantly shorter), shorter forearm (FLL) and less developed webbing (MTFF).

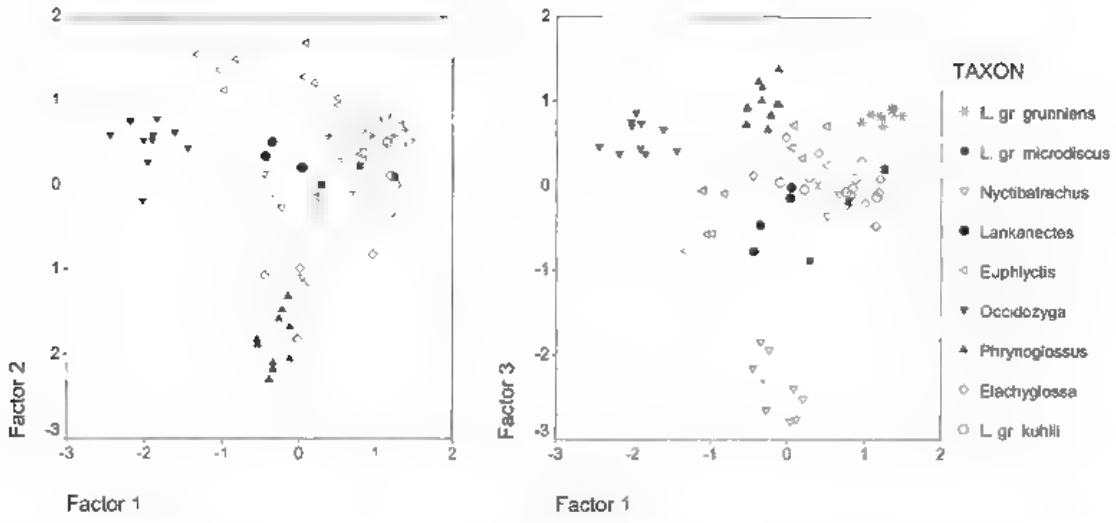

Fig. 2. Plots of multivariate analysis (first three axes) based on 22 measurements for the following nine genera, subgenera and species-groups of Asian Ranidae: *Euphlyctis*, *Lankanectes*, *Limnonectes (Elachyglossa)*, *Limnonectes (Limnonectes)* gr. *grunniens*, *Limnonectes (Limnonectes)* gr. *kuhlii*, *Limnonectes (Limnonectes)* gr. *microdiscus*, *Nyctibatrachus*, *Occidozyga* and *Phrynoglossus*.

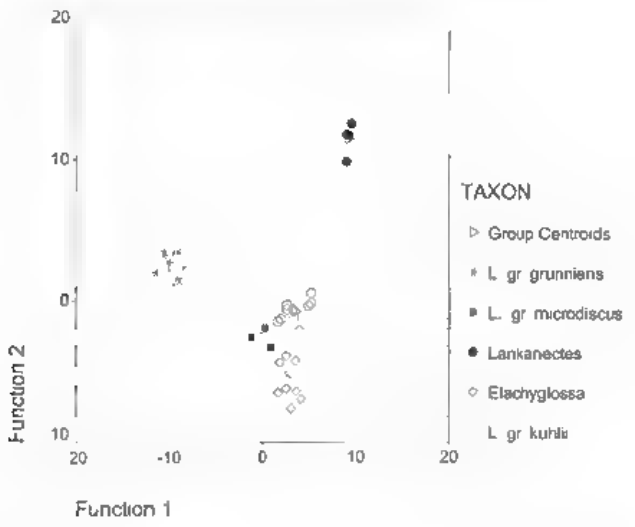

Fig. 3. Plots of discriminant function scores using minimization of Wilk's lambda of morphometric log-transposed characters (19 measurements) for the following five genera, subgenera and species groups of Asian Ranidae: *Lankanectes*, *Limnonectes (Elachyglossa)*, *Limnonectes (Limnonectes)* gr. *grunniens*, *Limnonectes (Limnonectes)* gr. *kuhlii* and *Limnonectes (Limnonectes)* gr. *microdiscus*.

Table 2 - Results of principal component analysis based on 22 ln-transposed measurements including specimens referred to the genera *Euphlyctis*, *Lankanectes*, *Limnonectes*, *Nyctibatrachus*, *Occidozyga*, and *Phrynoglossus*.

Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	19.991	90.870	90.870	10.520	47.819	47.819
2	1 148	5 219	96 089	7.154	32.518	80 338
3	0 260	1.181	97 270	3.725	16.932	97.270

Variable	Components for rotated component matrix			Variable	Components for rotated component matrix		
	1	2	3		1	2	3
SVL	0.670	0 635	0.374	FOL	0.630	0.623	0 427
HW	0.719	0 599	0.333	IN	0.951	0.230	0.132
HL	0.711	0 608	0 341	EN	0.699	0.571	0.397
MN	0 697	0.593	0.383	EL	0.702	0.605	0.460
MFE	0 698	0.583	0.388	TFL	0.564	0.720	0.366
MBE	0 605	0.596	0.468	MTTF	0.475	0.692	0.525
IFE	0 838	0 451	0 286	TFTF	0 814	0 497	0.334
IBE	0 831	0.504	0.165	MTFF	0 452	0 713	0.520
FLL	0.743	0.569	0.334	FFTF	0.852	0 405	0.208
HAL	0.589	0 694	0.392	IMT	0 700	0 483	0 460
TL	0.706	0.590	0.374	ITL	0 108	0 283	0 949

Specimens of the *microdiscus* species-group have a larger distance between eyes (IFE) and nostrils (IN) and their webbing is more incurved (TFTF). As to the differences existing to the other genera studied here, *Lankanectes* is larger (SVL) than *Nyctibatrachus*, its nostrils are more distantly separated; the inner metatarsal tubercle is smaller (IMT) in *Nyctibatrachus*, as is the webbing of the feet (MTTF, MTFF, TFTF) *Phrynoglossus* can be distinguished from the new genus by its smaller body size (SVL), its larger internarial distance (IN), its larger inner metatarsal tubercle (IMT) and its smaller webbing (MTFF, TFTF). Members of the genus *Occidozyga* show smaller distance between the eyes (IBE), longer hand length (HAL), a shorter inner metatarsal tubercle (IMT) and a longer inner toe (ITL) A smaller distance between the eyes and a smaller inner metatarsal tubercle separates *Lankanectes* from the members of the genus *Euphlyctis*

Table 3. Results of principal component analysis based on varimax rotated coefficients from log-transposed characters (25 measurements) for specimens referred to the genera *Euphlyctis*, *Fejervarya*, *Hoplobatrachus*, *Limnonectes*, *Minervarya* and *Sphaerotheca*.

	Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %
1	22.639	90.558	90.558
2	0.799	3.196	93.754
3	0 696	2.783	96.537

	Rotation Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %
1	10.152	40.610	40.610
2	9 597	38 390	78 999
3	4 384	17.538	96.537

	Components for rotated component matrix		
Variable	1	2	3
SVL	0 649	0 621	0.422
HW	0.617	0.706	0.337
HL	0 673	0 647	0.340
MN	0 667	0 646	0.330
MFE	0 649	0 674	0.322
MBE	0 639	0 683	0.312
IFE	0 505	0 768	0.371
IBE	0 553	0.757	0.368
FLL	0 589	0 682	0.419
HAL	0 661	0 653	0.346
TL	0 732	0 530	0.410
FOL	0.709	0 534	0 456
IN	0 235	0 817	0.471
EN	0 698	0 592	0.353
EL	0.599	0 691	0.351
TYD	0 712	0.487	0.367
TYE	0 449	0.773	0.223
TFL	0.654	0 635	0.364
FTL	0 757	0.415	0.484
MTTF	0 836	0 453	0 299
IFTF	0 349	0.349	0 859
MTFF	0 830	0.463	0.297
FFTF	0.432	0.402	0 788
IMT	0 419	0.797	0.293
ITL	0 873	0.304	0 283

Table 4 Some measurements and ratios of four specimens of *Lankanectes corrugatus*, including the lectotype (ZMB 4897) and the two paralectotypes (ZMB 62771-62772) from Rambodde (Sri Lanka), and a fourth specimen (MNHN 2000.0616) from Kandy (Sri Lanka) SVL is given in mm, all other measurements are given as per thousands of SVL. Sex and stages A, adult; J, juvenile; F, female; M, male.

Collection number	ZMB 4897	ZMB 62771	ZMB 62772	MNHN 2000 0616
Locality	Rambodde	Rambodde	Rambodde	Kandy
Sex and stage	AM	JF	AM	AF
SVL	44 0	37.2	33 5	44.4
HW	391	363	337	338
HL	382	379	379	354
MN	348	333	333	302
MFE	291	280	280	243
MBE	189	177	177	164
IFE	152	153	153	158
IBE	290	298	298	264
IN	56	70	66	66
EN	60	70	66	70
EL	119	138	106	108
FLL	195	210	185	191
HAL	200	199	224	218
TFL	96	127	120	115
TL	425	414	394	405
FOL	457	465	421	462
FTL	245	242	242	248
IMT	72	63	79	77
ITL	144	148	132	150
MTTF	311	328	310	296
MTFF	329	336	310	329
TFTF	129	124	141	139
FFTF	191	177	189	184

Distribution of some characters among several genera of Ranidae

Characters related with an aquatic mode of life

All anuran tadpoles show a lateral-line system on body and head, similar to that of fishes, i.e composed of rows of small pores opening on sense cells or neuromasts that are sensible to vibrations of low frequency in water (Noble, 1931: 318-321, Duellman & Trueb, 1985:

378-379). Most anuran species lose this system at metamorphosis, but it remains present in adults of a few anuran groups that have a mainly aquatic mode of life. This retention of a larval character in otherwise adult specimens is a case of partial paedomorphism (DUBOIS, 1987*a*). This is observed in several aquatic genera of anurans, distributed in various families, including the Discoglossidae (*Barbourula* Taylor & Noble, 1924, *Bombina* Oken, 1816), the Leptodactylidae (*Lepidobatrachus* Budgett, 1899) and the Pipidae (all genera) (fig. 4). In the Ranidae, which include various aquatic groups, some of them show the paedomorphic retention of lateral-line systems in adults, while others, which may seemingly appear as aquatic as the former ones, do not show this phenomenon. Three genera of Ranidae are known to retain the lateral-line system in adults: *Euphlyctis* (see e.g.: BOULENGER, 1920; DUBOIS, 1987*b*, 1992), *Occidozyga* Kuhl & Van Hasselt, 1822 (see e.g. DUBOIS, 1987*b*, 1992) and the new genus *Lankanectes* (fig. 4). To the best of our knowledge, the presence of a lateral-line system in adults of *L. corrugatus* has never been mentioned in the scientific literature, although these lines are quite obvious in live specimens (AD, personal observations) and usually remain visible, although not so easily, in fixed specimens.

DUBOIS (1987*b*) had considered the presence of a lateral-line system in adults as a synapomorphy of *Euphlyctis* and *Occidozyga*, which had led him to regard these two taxa as sister-groups and to treat them as subgenera of a single genus. Other characters which had supported this interpretation were the general body shape (*O. lima* looking almost exactly as a miniaturized *E. cyanophlyctis*), the shapes of the foot and of the extremities of digits, and the presence of continuous longitudinal white and dark stripes all along the rear part of the thighs (fig. 5). However, molecular cladistic data provided by MARMAYOU et al. (2000), KOSUCH et al. (2001) and DELORME et al. (submitted) strongly suggest that *Occidozyga* and *Euphlyctis* are not sister-groups, and that all or most of the characters listed above are convergences related to aquatic life. As a matter of fact, as mentioned above the lateral-line system is retained in adults of several aquatic frogs of other families and this is the case also of pointed digits and of fully webbed feet with a relatively short fourth toe.

As concerns the last character of the list above, the presence of longitudinal white and dark stripes on the posterior thigh is also observed in aquatic South-American hylid frogs of the genus *Pseudis* Wagler, 1830 (fig. 5) and, although less strikingly, in Chinese Ranidae that are also largely aquatic, i.e. *Rana (Pelophylax) plancyi* Lataste, 1880 and *Rana (Pelophylax) hubeiensis* Fei & Ye, 1982 (see e.g.: POPE, 1931: 511; FEI, 1999: 161). The meaning of this coloration character is not quite clear, but the fact that it appeared independently in several unrelated anuran groups having a largely aquatic life suggests that it also has an adaptive value for frogs with such a mode of life, probably as a camouflage device towards aquatic or aerial potential predators. In terrestrial frogs that live in grassland habitats, a striped dorsal pattern is often observed. These frogs have longitudinal lines either all along the middle of the back (vertebral stripe or band, present in many groups of frogs), or as several subparallel dark stripes on a brown dorsum. The latter, although perhaps less common, is also a rather widely distributed phenotype in frogs, observed e.g. in the Hyperoliidae (e.g., some *Afrixalus* Laurent, 1944 or *Hyperolius* Rapp, 1842), in the Ranidae (e.g., some *Ptychadena* Boulenger, 1917 or *Strongylopus* Tschudi, 1838), or in the Rhacophoridae/dae (e.g., some *Chiromantis* Boulenger, 1893 or *Polypedates* Tschudi, 1838). Such patterns can clearly contribute to a camouflage among herbs or elongated leaves. However in such frogs the rear parts of the thighs do not show longitudinal stripes. In terrestrial frogs the legs are not kept extended at

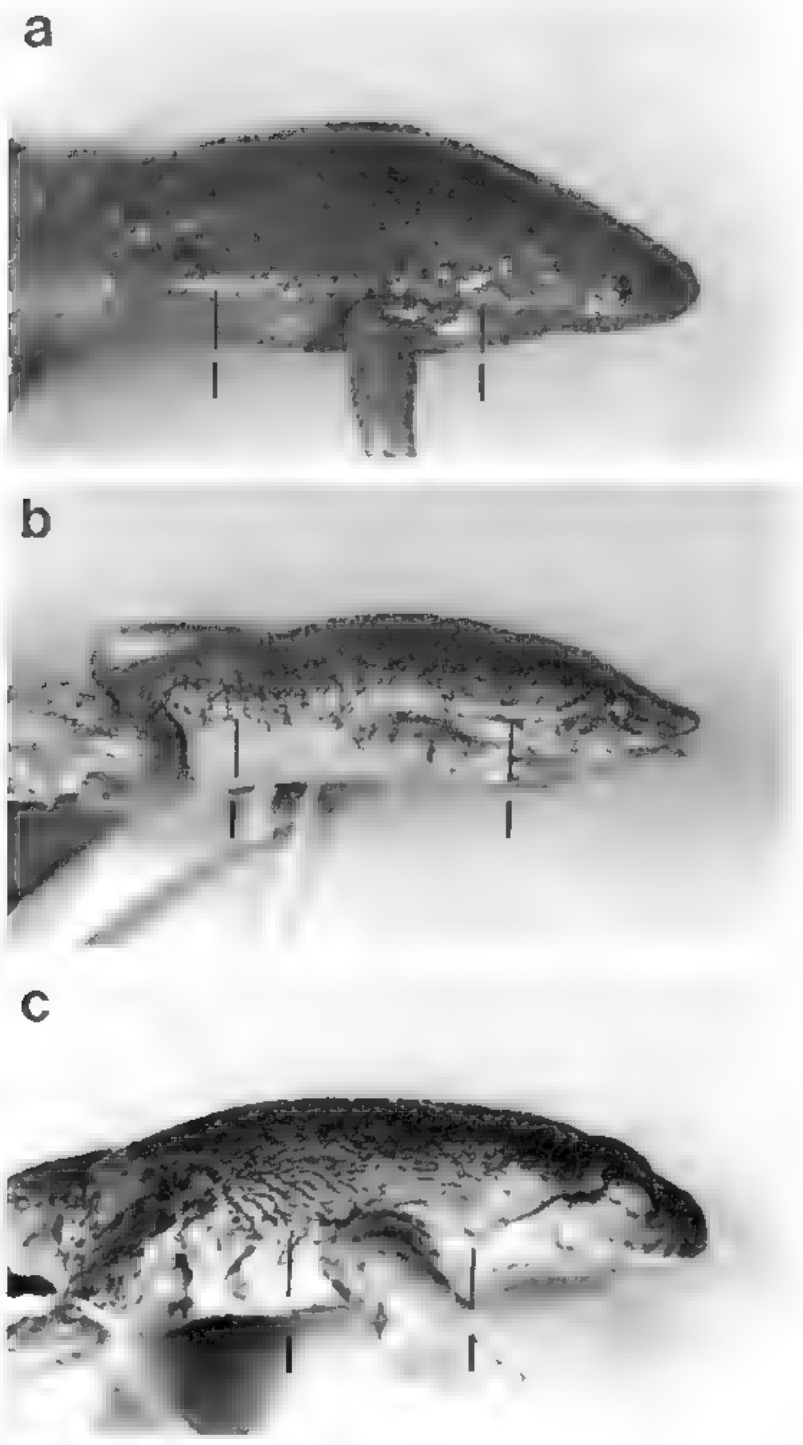

Fig. 4 — Lateral-line system (l) in several examples of aquatic anurans. (a) *Silurana tropicalis* Gray, 1864 (Pipidae, Silurannae), MNHN 1994.1915, adult male, Guinea. (b) *Occidozyga lima* (Gravenhorst, 1829) (Ranidae, Occidozyginae), MNHN 1999.6418, adult female, Yunnan. (c) *Lankanectes corrugatus* (Peters, 1863), MNHN 2000.0616, adult female, Sri Lanka.

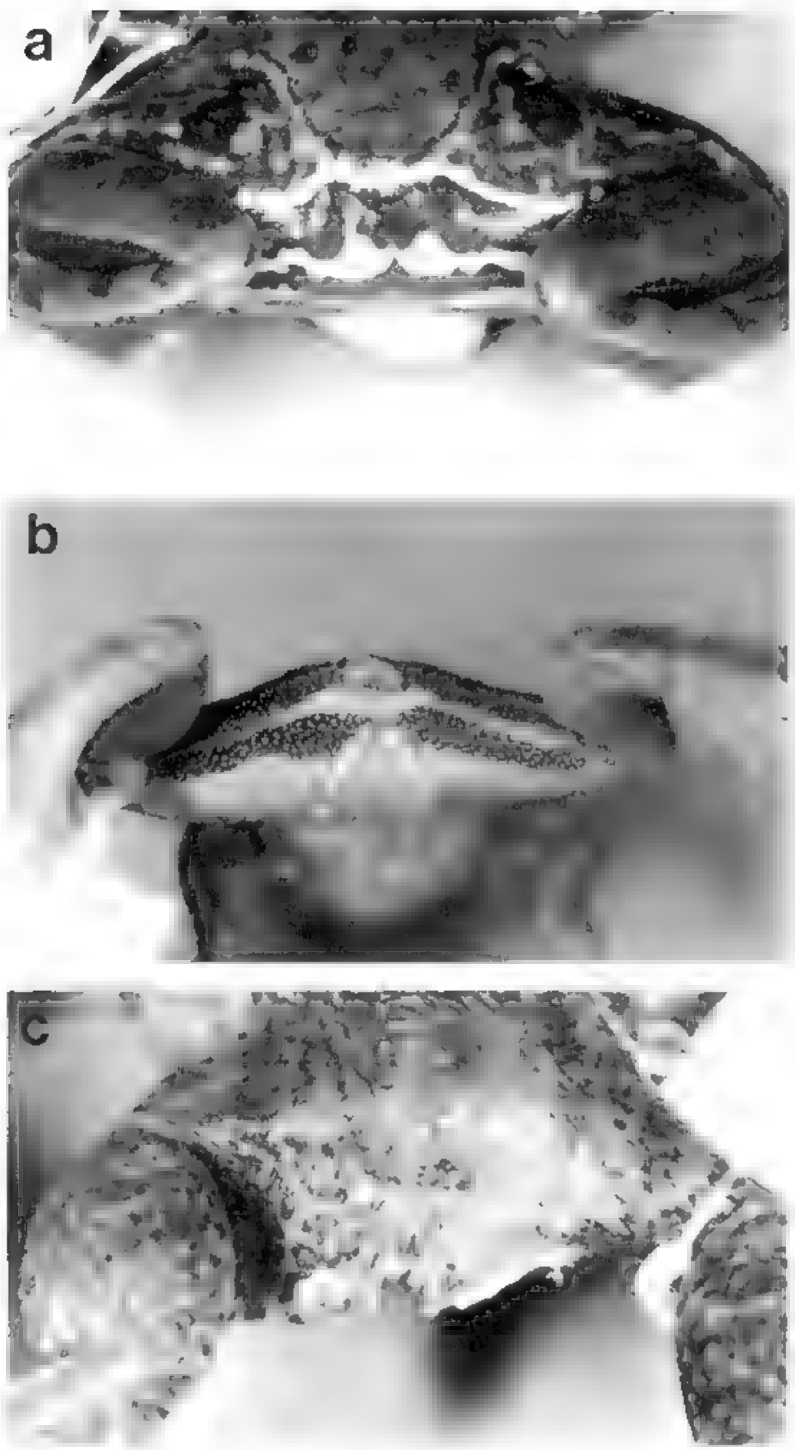

FIG. 5. Presence and absence of longitudinal white and dark lines on the back of thighs in several examples of aquatic anurans. (a) *Pseudis paradoxus* (Linnaeus, 1758) (Hylidae, Pseudinae), MNHN 1983.0390, juvenile female, Venezuela: lines present, (b) *Occidozyga lima* (Gravenhorst, 1829) (Ranidae, Occidozygmae), MNHN 1999.6418, adult female, Yunnan: lines present, (c) *Lankanectes corrugatus* (Peters, 1863) (Ranidae, Lankanectinae), MNHN 2000.0616, adult female, Sri Lanka: lines absent.

rest, so that the coloration of the back of thighs is not exposed: it is shown only during movements. In aquatic frogs, the situation may be different. These frogs, like *Euphlyctis* or *Occidozyga*, often remain suspended floating in water for some minutes or more, using the four limbs extended in the prolongation of the body or feebly bended laterally as balancers. In such a position the posterior surface of hindlegs is visible. If such a frog is then hidden within long and narrow aquatic vegetal structures, the longitudinal lines at the back of thighs might contribute to the camouflage, especially if it follows some other linear structures or coloration on the flank or dorsum of the frog, as well exemplified in the figure 16 of POPE (1931: 511). Although the new genus *Lankanectes* shares with *Occidozyga* and *Euphlyctis* the retention of lateral-line system in adults, it does not show the longitudinal stripes on the rear parts of the thighs (fig. 5) and this is a significant difference between the two genera (as well as between the closely related *Occidozyga* and *Phrynoglossus*). Perhaps this is connected to the fact that *L. corrugatus* usually inhabits shallow, mud-substrate (as opposed to gravel- or rock-substrate) streams, poor in vegetation (Pethiyagoda, personal communication).

Male secondary sex characters

Anurans display a large diversity of male secondary sex characters, including various kinds of spines, asperities and glands, vocal sacs and adult morphometric differences. The taxonomic significance of such dimorphic characters has no generality over the whole of anurans. In several groups, male secondary sex characters are diagnostic of species-groups, subgenera or genera, or even of higher taxa. this is e.g. the case of the pectoral plates of the megophryid tribe Oreolalagini (see DELORME & DUBOIS, 2001). In some other cases however, differences in such characters are species-specific and can even separate very similar and closely related species: examples include the presence/absence of nuptial spines in *Paa liebigii* (Günther, 1860) and *Paa vicina* (Stoliczka, 1872) (DUBOIS, 1976*a*, 1980) and the presence/absence of vocal sacs in *Polypedates leucomystax* (Gravenhorst, 1829) and *Polypedates mutus* (Smith, 1940) (SMITH, 1940; LIU & HU, 1961).

The major reason, besides general morphological resemblance, that apparently led BOULENGER (1920) to include *Rana corrugata* in the same group as *Rana kuhlii* seems to have been the presence in both species of "fangs" at the front of the lower jaw (fig. 6). This character was also used by EMERSON & WARD (1998) and EMERSON et al. (2000) as the basis for the vernacular name of "fanged frogs" which they gave to the genus *Limnonectes*. However, not all frogs of this group possess fangs (see e.g., BOULENGER, 1920, SMITH, 1922*a-b*, BOURRET, 1942), and this vernacular name does not appear more appropriate for these frogs than that of "voiceless frogs", the previous name used by the same authors (EMERSON & VORIS, 1992, EMERSON & BERRIGAN, 1993). As a matter of fact, even if several species of South-East Asian frogs of this group are devoid of structurally differentiated vocal sacs, they are not voiceless, as their males can emit advertisement calls, as was observed in *Limnonectes blythii* (MATSUI, 1995), or at least loud territorial calls, as was observed in *Limnonectes* cf. *kuhlii* (AD & AO, unpublished observations, see below). As for *Lankanectes corrugatus*, males show differentiated vocal sacs and emit loud calls (AD, personal observations, Sri Lanka, June 1999) whose function has to be clarified, given that they persist after the breeding season (Pethiyagoda, personal communication), but which probably can have an advertisement function, possibly combined with a territorial one.

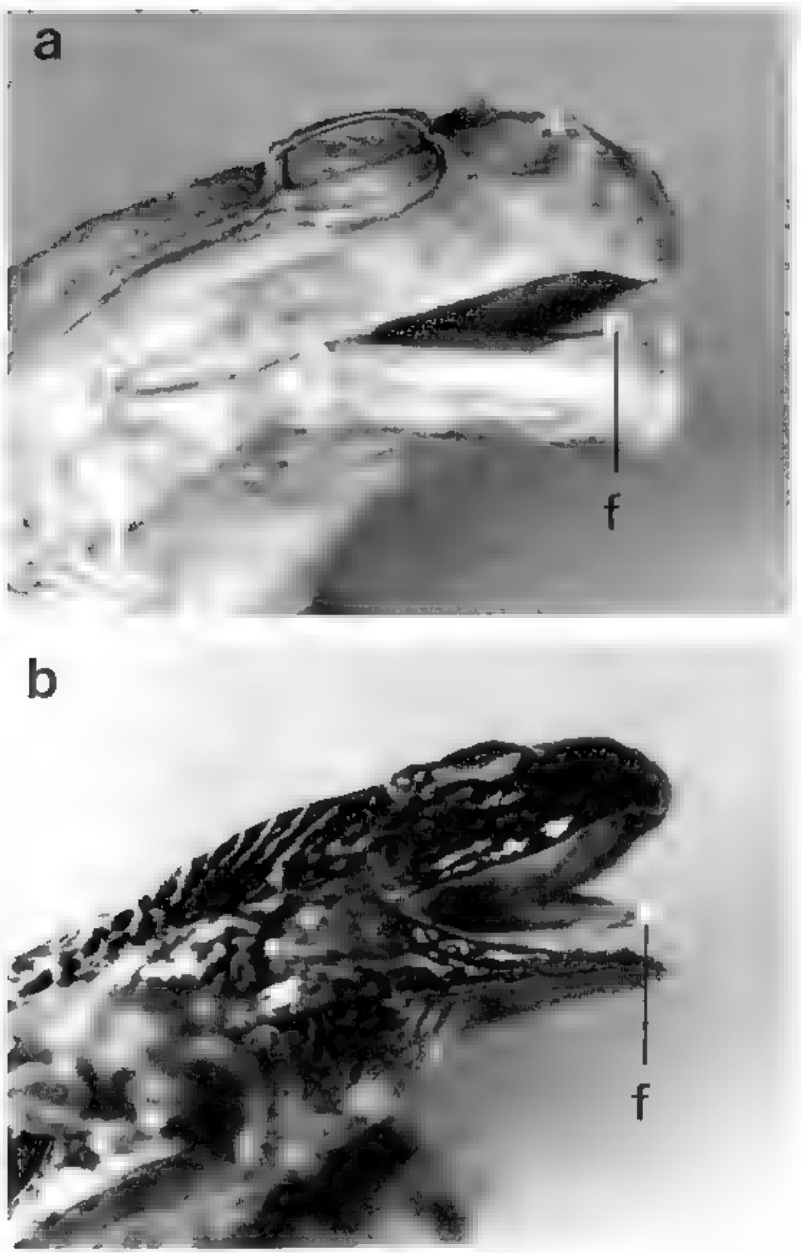

Fig 6 Fangs (f) at front of lower jaw in two Asian ranid groups. (a) *Limnonectes* (*Limnonectes*) cf *kuhlii* (Tschudi, 1838) (Ranidae, Dicroglossinae), MNHN 1938.0030, adult male, Vietnam, (b) *Lankanectes corrugatus* (Peters, 1863) (Ranidae, Lankanectinae), ZMB 4897, adult male, lectotype, Sri Lanka

As mentioned above, fangs are present in adult males of some species of *Limnonectes* only. These species also tend to have a much wider head in males than in females, and in some of them (some of the members of the subgenus *Elachyglossa*) they also show a knob on the dorsal back of head, starting between the eyes and extending beyond them (SMITH, 1922*a-b*;

BOURRET, 1942). We regard all these characters (fangs, wide head, dorsal cephalic knob) as related to agonistic behaviour between males, like in several other cases of spines and other differentiated structures on the heads of males (see e.g.· SHINE, 1979; DUBOIS & OHLER, 1998). In the Siriphum agricultural station of the Doi Inthanon in northern Thailand, in the night of 24 September 1986 we had the opportunity to observe an adult male of *Limnonectes* cf. *kuhlii* that, disturbed by our foraging in water with a small net to collect tadpoles, suddenly emitted a loud and deep territorial call, "*koaa, koaa*", and repeated it several times. While emitting this guttural whistling, this frog had its body immersed in water but its head was raised above the water level, and quite voluntary so as the frog was leaning on a rock and the fore part of its body was raised on its stretched arms. Seen from the level of the surface of water, this large head evoked a much larger frog than the actual size of this male (MNHN 1987.3197, SVL 63.7 mm; HW 28 6 mm, HL 29.6 mm) On several occasions, in Thailand, Laos and Vietnam, we had the opportunity to observe and collect very large-headed males of *Limnonectes* cf. *kuhlii*. However, on every occasion we were struck by the fact that, in a given station (e.g , a small pond, or a portion of several meters along a small stream), we never found more than one such large-headed male, although other males may have been seen there· all other males collected along with the latter had a "normal" or only slightly enlarged head, although some of them were of a size similar to that of the large-headed male of the station We suggest a possible interpretation for these observations. in each station, a single male might occupy the hierarchical position of a dominant male. This male would develop a very enlarged head but its presence, and most likely also its behaviour (with territorial calls and possibly also fighting with other males) would inhibit the development of enlarged head in all other males nearby The existence of such an inhibition in dominated males, which could likely be implemented through a hormonal mechanism, could rather easily be submitted to experimental testing, and this could be done by scientists living in countries where these frogs occur.

These observations suggest that, unless large series of specimens are available for study, it is impossible to be sure of the "maximum" development of male sex characters (including the length of the fangs, the width of the head or the size of the cephalic knob) in any species or population of *Limnonectes*. It is therefore advisable to look for other characters to distinguish species, because, when only the development of male sex characters is available in this respect, these characters may be misleading, being in part due to the studied males occupying a dominant or dominated position in the hierarchy of the group. This remark holds particularly true for frogs of the subgenus *Elachyglossa*, that show a very variable development of the cephalic knob (SMITH, 1922*a-b*; BOURRET, 1942) However, despite these remarks, it should be stressed that, even in those males that do not show a "much enlarged head", the head is significantly proportionally wider in males than in females (OHLER & DUBOIS, 1999).

As concerns the species *Lankanectes corrugatus*, very few museum specimens are available for study outside Sri Lanka, and little is known on its variation, including sexual dimorphism in size and other measurements. No detailed measurements of this species were provided in the two books dedicated to the Sri Lankan frogs by local zoologists (KIRTISINGHE, 1957; DUTTA & MANAMENDRA-ARACHCHI, 1996) BOULENGER (1920) provided measurements for 4 specimens in the London museum, including 3 adult males and 1 female. We provide in tab. 1 our measurements of 4 other specimens, 2 males and 2 females, in the Berlin and Paris museums, including the 3 original syntypes of the species. According to this very limited material, no sex dimorphism appears to exist in this species for either the total size or

the size of head, but this sample is much too small to permit definitive statements in this respect. However, given the limited information currently available, this species would appear to differ from *Limnonectes* in not exhibiting sex dimorphism in the size of head.

While the male secondary sex characters discussed above are exceptional in anurans, two other male characters are very widely distributed in many anuran groups, i.e. the presence of nuptial pads (usually covered with a layer of minute spines) on the first finger (and sometimes also on the prepollex, the second and the third fingers) and the presence of vocal sacs with openings on the sides of the mouth floor. The first of these characters is absent both in *Lankanectes* and in all frogs of the tribe Limnonectini of the Dicroglossinae, i.e. the genera *Limnonectes* and *Taylorana*. As for the second character, as mentioned above, so-called "voiceless" frogs of the genus *Limnonectes* can emit loud territorial calls whose function is probably to keep other males at distance. Some at least of them are known to emit also advertisement calls, i.e. calls whose function is to attract females during breeding. Some members of this genus, as currently understood, do have internal vocal sacs, while others lack them. *Lankanectes corrugatus* produces dull advertisement calls that are very striking for anyone who meets these frogs in the field and that can be heard from several meters in the forest habitat (AD, personal observations), they are evoked by DUTTA & MANAMENDRA-ARACHCHI (1996: 82) as "*Urrm.* ". The presence of vocal sacs in these frogs, which had been ignored by GÜNTHER (1864) and BOULENGER (1890, 1920), was noted by KIRTISINGHE (1957) and DUTTA & MANAMENDRA-ARACHCHI (1996).

Other characters

Three final characters related to reproduction may briefly be mentioned here. The first one is parental care, listed by EMERSON et al. (2000) in their "definition" of the genus *Limnonectes*. However, according to currently published observations (ALCALA, 1962, INGER, 1966, 1985, INGER et al., 1986; INGER & VORIS, 1988; EMERSON, 1996; INGER & STUEBING, 1997; BROWN & ISKANDAR, 2000), parental care is only known in some species of the *Limnonectes microdiscus* group of the nominative subgenus *Limnonectes* (sensu DUBOIS, 1987*b*) and cannot be included among the characters diagnostic of the whole genus *Limnonectes*, at least as currently understood. According to ISKANDAR (in EMERSON, 1996, see DUBOIS, 1999), a species of this group shows endotrophic development of embryos within the genital tract of the female. In another group of Limnonectini, the genus *Taylorana*, direct development occurs in eggs laid in terrestrial nests (TAYLOR, 1962; OHLER et al., 1999). All these observations confirm the tendency that exists in this group for correlative increase of the size of eggs with reduction of their numbers, leading eventually to direct development or ovoviviparity, a tendency already identified by DUBOIS (1975).

A second interesting character is the position of the arms of the male during amplexus. Although this has never been mentioned in the literature, we observed on various occasions (AD & AO, unpublished observations, briefly mentioned in MARMAYOU et al., 2000: 295) that in the species *Phrynoglossus martensii* Peters, 1867, type-species of *Phrynoglossus* Peters, 1867, amplexus is lumbar, not axillary. This is a strong reason, added to the morphological ones (SMITH, 1931; TAYLOR, 1962; OHLER & DUBOIS, 1999) for considering *Occidozyga* as a genus distinct from *Phrynoglossus*, and not as a synonym of the latter, as suggested by some authors (INGER, 1954, 1966, 1996), or even as a subgenus of *Rana* (EMERSON & BURRIGAN, 1993).

Another peculiarity of *Phrynoglossus* is its unpigmented eggs, that most likely are deposited under some shelter, but, to the best of our knowledge, reproduction and egg-laying has never been described in this genus. The amplectic position of *Lankanectes corrugatus* has never been observed so far (Pethiyagoda, personal communication). As for the eggs, in this species they are pigmented, thus differing from those of *Phrynoglossus*.

Conclusion: taxonomic allocation of the new genus

We presented above in tab. 1 a list of characters that we consider diagnostic of the genera *Euphlyctis*, *Lankanectes*, *Limnonectes*, *Nyctibatrachus*, *Occidozyga*, *Phrynoglossus* and *Taylorana*. All these genera have in common the presence of a forked omosternum, that distinguishes them from the Raninae. However, the phylogenetic data recently provided by several teams (Bossuyt & Milinkovitch, 2000; Vences et al., 2000; Delorme et al., submitted) suggest that these seven genera must be referred to several subclades within the Ranidae, which we taxonomically treat as distinct provisional subfamilial taxa. (1) *Euphlyctis*, *Limnonectes* and *Taylorana* are members of the Dicroglossinae Anderson, 1871; (2) *Occidozyga* and *Phrynoglossus* are members of the Occidozyginae Fei, Ye & Huang, 1991; and (3) *Nyctibatrachus* is a member of the Nyctibatrachinae Blommers-Schlösser, 1993. As for *Lankanectes corrugatus*, the cladistic data available (Bossuyt & Milinkovitch, 2000; Vences et al., 2000; Delorme et al., submitted) suggest not only that it belongs in a genus distinct from *Limnonectes*, but also that it cannot be maintained in the subfamily Dicroglossinae. For the time being, given the data of Bossuyt & Milinkovitch (2000) and Vences et al. (2000), the closest relatives of this genus would appear to be the subfamilies Raninae and Nyctibatrachinae, but both groups exhibit characters widely different from those of *Lankanectes*. From the Raninae, *Lankanectes* differs readily by its forked omosternum and by a completely different general habitus. As for the Nyctibatrachinae, except for the forked omosternum the new genus only shares with *Nyctibatrachus* a few derived characters presumably related to the aquatic mode of life of both genera (general body shape, short legs, short internarial distance), but both genera show significant differences in a number of other characters (extremities of digits, lateral-line system in adults, network of ridges on dorsal parts, femoral glands, fangs and nuptial pads in males, tadpole keratodont formula), which do not support the inclusion of the new genus in the Nyctibatrachinae. The only solution for the time being is to refer the new genus to a new provisional suprageneric taxon, which, as well as all other such taxa, will have to be tested by subsequent works (for more details, see Dubois, 1999).

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APPENDIX I

COMPARATIVE MATERIAL EXAMINED

Specimens marked with an asterisk (*) are those which were used for the morphometric analyses (tab. 2-3, fig. 2-3)

Euphlyctis cyanophyctis (Schneider, 1799) NEPAL. *Dillikot*, 2400 m. MNHN 1975.2164*, 1975 2182*-2183*, 1975.2194*, 1975.2196*, *Samchare* MNHN 1977 1364-1403, *Sukhet*, 900 m. MNHN 1996 9274-9280; *Tatopani Khola*, 2200 m MNHN 1975.2250-2273.

Euphlyctis hexadactylus (Lesson, 1834). – INDIA: NMW 2512.1*-5*, 25121*.

Limnonectes (Elachyglossa) doriae (Boulenger, 1887). MYANMAR *Mount Carin*, 900-1000m MNHN 1893.435*-437*.

Limnonectes (Elachyglossa) gyldenstolpei (Andersson, 1916) - LAOS Ban Tap, Bokeo MNHN 1997 4149*-4152* – THAILAND *Bang Hue Pong, Koon Tan Mountains, Lamphun Province* NRM 1656*, holotype, *Phu Kradung Samkokpai, 860-870 m, Loei Province* MNHN 1987 3132*.

Limnonectes (Elachyglossa) toumanoffi (Bourret, 1941) - CAMBODIA: MNHN 1948.126*, holotype.

*Limnonectes (Limnonectes) (*gr *grunniens) blythii* (Boulenger, 1920) - THAILAND *Khao Phra Tiu* MNHN 1986.3154*-3168*

*Limnonectes (Limnonectes) (*gr *kuhlii) cf kuhlii* (Tschudi, 1838). – INDONESIA. *Sumatra, Sidikalang* MV 80*, MV 82*, MV 102*-103*, MV 105*, MV 108*, MV 111*-112*, MV 117*, MV 127* – THAILAND *Doi Inthanon*: MNHN 1987 3197. – VIETNAM: *Tonkin*: MNHN 1938 0030.

*Limnonectes (Limnonectes) (*gr *microdiscus) leytensis* (Boettger, 1893) PHILIPPINES Dumaguete: MNHN 1964.0283*

*Limnonectes (Limnonectes) (*gr *microdiscus) woodworthi* (Taylor, 1923) – PHILIPPINES *Baybay*: MNHN 2000 0611*-0612*

Nyctibatrachus beddomei Boulenger, 1882 INDIA *Tinnevelly* BMNH 1882 2 10 27-30*, NHMB 1271*

Nyctibatrachus humayuni Bhaduri & Kripalani, 1955 INDIA. BMNH 1958 1 4 25*-26*

Nyctibatrachus deccanensis Dubois, 1984 INDIA *Anamallays* BMNH 1947 2 4.47*, 1947 2 4 49*, 1947.2.4.52*, 1947.2.4.55*, syntypes of *Rana pygmaea* Günther, 1876

Occidozyga lima (Gravenhorst, 1829) CAMBODIA BMNH 1861 4 12 31*-32*. CHINA. BMNH 1932 5 1 2*, holotype of *Houlema obscura* Gray, 1831. INDONESIA *Java* BMNH 1844.2 22 94A*-94C* THAILAND *Siam* BMNH 1859 7 1 36*-39* CHINA *Jinghong, Yunnan Province* MNHN 1999 6416* 6422*.

Phrynoglossus magnapustulosus Taylor & Elbel, 1958 CHINA *Jinghong Yunnan Province*. MNHN 1999 6442-6453.

Phrynoglossus martensii Peters, 1867. THAILAND. Khao Chong, Trang Province MNHN 1987 2894*, 1987 2898*, 1987 2907*, 1987 2915*, 1987 2925*, 1987 2934*, 1987 2938*, 1987 2940*, 1987 2958*, 1987.2960*

Pipa carvalhoi (Miranda-Ribeiro, 1937). – BRAZIL. *Bahia*. MNHN 1981.298-299.

Pseudis paradoxus (Linnaeus, 1758) – VENEZUELA: *Montecal*: MNHN 1983 0390.

Rana (Pelophylax) habetensis Fei & Ye, 1982 CHINA *Zhejiang* MNHN 1931 0064-0066

Silurana tropicalis Gray, 1864 GUINEA *Mount Nimba, Region of N'Zo* MNHN 1944 0162-0164, 1994 1907-1927

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